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Mollusc abundance and associations in Leschenault Inlet estuary

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Abstract

Five years of abundance data for the molluscs of the Leschenault Inlet estuary at 22 sites were analysed to provide preliminary results on patterns of their temporal and spatial variably and their potential associations. Only a limited number of the most commonly occurring species were selected for analysis, and only those collected in February and May for each year 1983-1986 were analysed to provide a consistency of sampling times and places, and to compare results in the same season. The spatial and temporal variation of the mollusc species showed species responded to a south-to-north, along-estuary salinity gradient, and to time. The species were assigned to two groups on the basis of their responses to the intra-estuarine gradient. The first group, *Arthritica*, *Acteocina*, *Hydrococcus* and *Tellina*, generally increased in abundance to the north, though the increases varied markedly between the four species, with *Arthritica* showing least variation between sites, *Tellina* showing a large between-site effect, and *Acteocina* and *Hydrococcus* showing marked effects of site differences. *Arthritica* and *Tellina* decreased in abundance over time whereas the other two species showed little change over time. The second group, *Bedeva*, *Nassarius* and *Spisula*, had a negative response to the south to north gradient *i.e.* abundance decreased markedly, especially for *Nassarius* and *Spisula* as the salinity increased. *Nassarius* and *Spisula* also markedly decreased in abundance over time. There is only a slight decrease in abundance over time for *Bedeva*. Cluster analyses showed year to year changes in mollusc associations, signalling caution in the use of such mathematical approaches to categorize biotic assemblages within complex environments such as estuaries with marked hydrochemical and biotic dynamism.

Keywords: Leschenault Inlet, south-western Australia, estuary, molluscs, mollusc abundance, mollusc associations, cluster analyses.

Introduction

The molluscs of the Leschenault Inlet estuary are variable in their patterns of distribution and abundance through time and space, with the different species generally exhibiting independent patterns of population dynamics both within a given year, and over a number of years (Semeniuk & Wurm 2000). This variability occurs against a back-drop of a seasonally dynamic hydrology, and within a framework of generally medium-term stable estuarine habitats. The spatial and temporal variability and independence between species renders it difficult to consider the fauna in terms of formal "communities" and to rigorously analyse population dynamics.

The sampling in the Leschenault Inlet estuary undertaken by T A Semeniuk, P A S Wurm and V Semeniuk during 1982-1987 (Wurm & Semeniuk 2000; Semeniuk & Wurm 2000; T A Semeniuk 2000; Deurr & Semeniuk 2000) resulted in a large data set on the biota and their environmental setting, involving 22 field sites, 32 sampling times (temporarily stratified), and eight environmental parameters. Specifically for the molluscs, there were 32 species of mollusc, and for three species there were size/frequency data at each sampling time for each sampling site. The full set of data are currently being systematically analysed, and this will be the subject of a later more comprehensive paper on mathematical techniques appropriate to the analysis of the data, and the resulting trends. However, to provide an indication of patterns of mollusc population dynamics and associations, beyond that provided in Semeniuk & Wurm (2000), a series of preliminary analyses of the data are presented in this paper.

The objectives of this paper are twofold: 1) determine any 5-year trends in population patterns for selected species against the salinity and habitat framework of the estuary; and 2) determine the possible associations of molluscs in the Leschenault Inlet estuary. In this context, this paper supplements the information on molluscs presented at a descriptive level by Semeniuk & Wurm (2000).

Setting

Study Area

Leschenault Inlet is an elongate shallow water estuary in south-western Australia. It has distinctive patterns of hydrodynamics and hydrochemistry, bathymetry and sediment types, features that are useful to differentiate habitats for benthos. Its waters are poikilosaline, with an interplay between daily tide-derived marine water through "The Cut", winter freshwater influx from rivers, run-off, drains and seepage, and summer evaporation. The water body is divided into 4 salinity fields based on mean salinity and its annual variation (Fig 1; after Wurm & Semeniuk 2000):

1. a deltaic field, with salinity varying from hyposaline to mesosaline; mean salinity is slightly less than sea water, with a large variability about the mean;

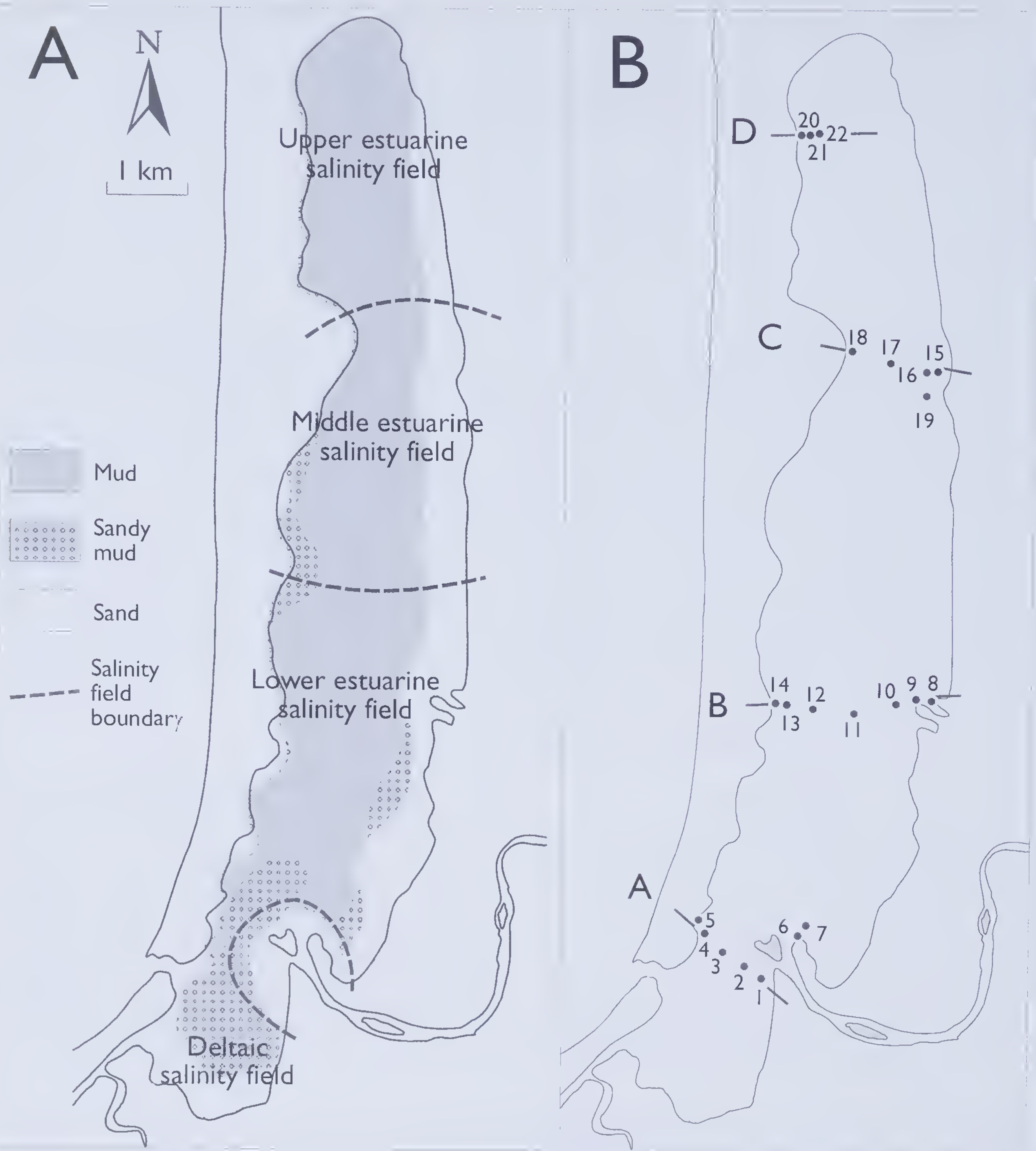

Figure 1. Maps of Leschenault Inlet showing; **A:** the nature of the estuarine salinity fields oriented south-north within the system; and **B:** the location of the sample sites (after Wurm & Semeniuk 2000).

2. a lower estuarine field, with salinity mainly mesosaline; mean salinity is slightly greater than sea water, with a small variability about the mean;
3. a mid estuarine field, with salinity fluctuating within the mesosaline range; mean salinity is higher than sea water, with a large variability about the mean; and
4. an upper estuarine field, with salinity varying annually from hyposaline to hypersalinity; mean salinity is much greater than sea water, with a very large variability about the mean.

In terms of bathymetric setting and substrates, the estuary is divided into several units (Wurm & Semeniuk 2000), four of which are relevant to the background of this paper (Fig 1): 1) a relatively deep water central basin, underlain by mud; 2) a northern shallow water subtidal to tidal flat, underlain by mud; 3) a tidal to shallow water western platform/ramp underlain by muddy sand; and 4) an eastern tidal to shallow water platform underlain mainly by sand.

On the basis of estuarine salinity, bathymetry, and substrates, the estuary can be divided into small-scale habitats (Wurm & Semeniuk 2000). These habitat units provide a framework within which the molluscan fauna were sampled.

The molluscan fauna and their habitats

Thirty two species of mollusc have been recorded in Leschenault Inlet (Semeniuk & Wurm 2000). Six species were common: *Arthritica semen, Tellina deltoidalis, Nassarius burchardi, Spisula trigonella, Hydrococcus brazieri,* and *Acteocina* sp. An additional seven species were present more or less throughout the estuary: *Assiminea* sp *Bedeva paivae, Bittium granarium, Irus crenata, Sanguinolaria biradiata, Solemya australis*, and *Xenostrobus securis*, though not abundant at all times or abundant only sporadically. Generally the molluscs inhabited tidal sand or tidal mud, shallow water platform sand or muddy sand, or deep water basin mud, within lower, middle or upper estuarine salinity fields.

Although present relatively consistently throughout the estuary, and in sufficient numbers to enable description and comparison over five years of study, the six main mollusc species were not always abundant (Semeniuk & Wurm 2000). At times, there were major temporal increases and fluctuations in density of populations, from hundreds or thousands of individuals in a square metre, to zero or less than ten individuals, often with patchiness in abundance resulting in large variance around the mean density for a given site. These fluctuations for the various species were not synchronous. Also, there were times when the density for given species did not markedly vary in time.

Methods

Field methods

The 22 sampling sites of Wurm & Semeniuk (2000) were used in this study. These are numbered 1-22, arrayed along four transects, A, B, C and D that correspond to locations within the four estuarine salinity fields *i.e.* Transect A is in the deltaic salinity field, Transect B is in the lower estuarine salinity field, Transect C is in the middle estuarine salinity field, and Transect D is in the upper estuarine salinity field (Fig 1). Individual sampling sites thus carry notation of transect location and sample site number *e.g.* Site B11 is sample site 11 located along Transect B.

Semeniuk & Wurm (2000) describe two methods for sampling molluscs. All species except *Arthritica semen* were sampled with a square box-corer of size 25 cm x 25 cm x 25 cm. *A. semen*, because of its small size and high abundance, was sampled with a metal cylindrical corer of 10 cm diameter and 15 cm length (to make its abundances comparable to the other molluscs for analysis, the numbers of *Arthritica* in the small corer were multiplied by 7.9). From each site within a habitat, five replicate samples were collected within an homogeneous area of 5 m radius. Because of the large number of sampling sites, involving field surveys and laboratory sorting time, the 22 field sites were variably and selectively sampled during 1982-1986 as follows: sites A2, A3, A4, B9, B11, B11, C15, C19, C17, D20, D21 and D22 were sampled quarterly, and A1, A5, A6, A7, B8, B10, B13, B14, C16 and C18 were sampled annually (Wurm & Semeniuk 2000).

Analytical methods

The full data set in this study encompasses 22 field sites, 32 sampling periods, 32 species, and eight environment parameters (habitat setting, water depth, % mud content in the substrate, salinity, temperature, oxygen concentration, presence of seagrass/algae), resulting in a complex system to analyse. It was decided to trim the data base, selecting the most important attributes, to highlight the results of any numerical classification procedure. Data were analysed using two principal methods, *viz* analyses of abundance trends spatially and temporally after various transformations, and agglomerative hierarchical cluster analyses using Fexible UPGMA to determine relationship of molluscs to environmental setting and possible assemblage associations. Data on mollusc numbers are presented in Appendix 1. A fuller data set is presented in Wurm (1987) and Semeniuk & Wurm (2000).

For the analyses of abundance trends both spatially and temporally, the data used were records for 13 species at 22 sites over 11 sampling times. The values recorded are mean occurrences of each species. The data analysis was carried out in a number of stages. The initial inspection of the data reduced the 13 species to the 7 most abundant species: 1) *Acteocina* sp; 2) *Arthritica semen*; 3) *Bedeva paivae*; 4) *Hydrococcus brazieri*; 5) *Nassarius burchardi*; 6. *Spisula trigonella*; and 7. *Tellina deltoidalis*. Of the 22 sites, only 12 sites (A2, A3, A4; B9, B11, B12; C15, C17, C19; and D20, D21, and D22) were analysed for the 11 sampling times as they were the only sites with complete information for all species and times. The sampling times used were: February 1982, May 1982, February 1983, May 1983, February 1984, May 1984, February 1985, May 1985, February 1986, May 1986, February 1987. For further analyses the sites were grouped into four classes (A, B, C, and D) which are indicative of their locations within the estuary, and hence the salinity levels.

The subsequent analyses first considered all three factors: species (7), sampling times (11), and sites (12), and the three possible two-way interactions, then reduced the sites (4 classes) and the times to linear components. The means for each species classified by the three factors was analysed using a linear model with S-PLUS (Venables & Rippley 1994). Since the data were mean values, the error distribution used was Gaussian, and analysis of residuals was used to confirm the distributional assumptions. If the primary individual counts of occurrences were used, the data could have been analysed as a generalised linear model (GLM) with a Poisson error distribution (McCullagh & Nelder, 1983), but this will be the subject of a later more comprehensive paper.

The analysis of standardised residuals shows significant departures from normality, and a plot of the residuals *vs* fitted values suggested that the variation increases with the mean value, indicating that a logarithmic transformation of the data may be appropriate. The analysis of the raw data was not considered further. Full analysis was of logarithmic transformed data in the form y = log (mean + 0.05). The addition of a small value (0.05) to the raw means was made to overcome the problem of taking the log of zero values. Further analyses using reduced levels of the factors, such as grouping the sites and identifying linear components of time and site (a surrogate for the salinity gradient), were undertaken to highlight the trends in time and/or salinity and their effects on the mean occurrences of the species. Analysis of site groups, where the 12 sites are regrouped into four classes (A, B, C, and D), was used to reflect the salinity gradient within the estuary. Analysis of a linear trend in the four site classes, where the 4 site classes (A - > 1, B- > 2, C - > 3, and D - > 4) were used to indicate that there is a gradient dependent on site class *i.e.* a salinity trend up (down) the estuary. The process of linear trend analysis was further simplified by reducing the 10 degrees of freedom for time to a linear trend over time. The times were "ordered" so that positive (or negative) linear trends for time would indicate increases (or decreases) in overall species occurrences over time. Interactions, especially of species with time, would indicate that species occurrences are not consistent across time(s) for all species *i.e.* some species may decrease over time while others remain stable or even increase. The final linear model included main effects of species, time trend, and site class trend, with interactions of species with time trend and species with site class trend. No other effects have been included.

Only data from the February surveys between 1983 and 1986 were analysed using agglomerative hierarchical clustering (Flexible UPGMA of PATN) in which equal weight is given to objects not groups (Everitt 1974; Belbin 1995) used in this analysis, since during these surveys all 22 sites were consistently sampled and thus enabling comparison of data between comparable seasons. The eight most abundant or relatively consistently present mollusc species were used, *viz Acteocina* sp, *Arthritica semen, Bedeva paivae, Bittium granarium, Hydrococcus brazieri, Nassarius burchardi, Spisula trigonella* and *Tellina deltoidalis.*

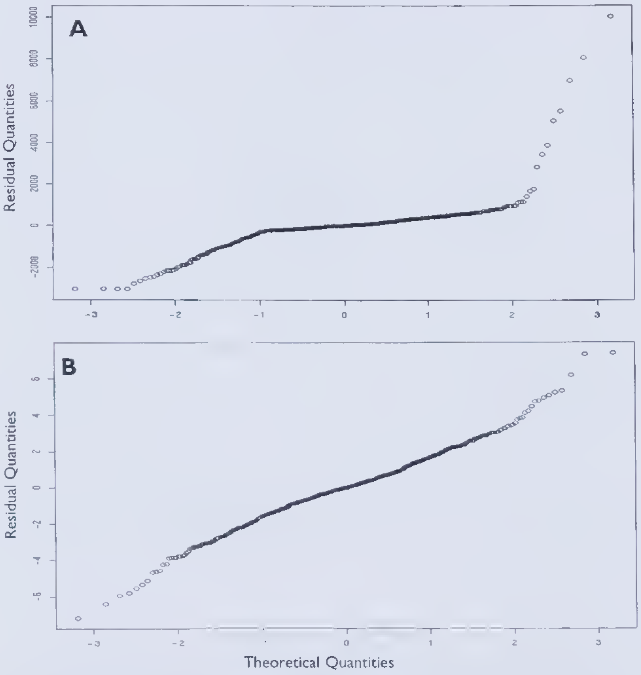

Figure 2. A: Residual analysis for untransformed mean occurrences of mollusc species. **B:** Residual analysis for Log Transformed Mean Occurrences

For the clustering analysis, the following information was used: each category of environmental parameter was assigned its actual numerical value, or where a parameter had a range of qualities or values, or to a class category: year (*e.g.* 1983); site (*e.g.* site B11); depth (actual field measurement); estuarine salinity field assigned to a class I = deltaic field, II = lower estuarine field, III = mid estuarine field, IV = upper estuarine field); % content of mud in the substrate (actual value); seagrass assigned to a class 0, 1 or 2; *Chaetomorpha* assigned to a class (0 = if absent, 1 = present but patchy, 2 = present and continuous or abundant); mollusc species (mean number of individuals in a square metre based on five replicates for each of the eight species sampled).

During data processing, since zero scores for abundances were inadmissible to the programme, specific sites and species, in which there were no biota for a given year, or the species were generally absent through the estuary for that year, respectively, were excluded. For 1983, data included *Arthritica semen, Bedeva paivae, Hydrococcus brazieri, Nassarius burchardi, Spisula trigonella,* and *Tellina deltoidalis* for all sites, and *Acteocina* sp *Bittium granarium* were excluded. For 1984, data included *Acteocina* sp, *Arthritica semen, Bedeva paivae, Hydrococcus brazieri, Nassarius burchardi, Spisula trigonella,* and *Tellina deltoidalis* for 21 sites, and *Bittium granarium* and site A1 were excluded. For 1985 data included *Acteocina* sp, *Arthritica semen, Bedeva paivae, Bittium granarium, Hydrococcus brazieri, Nassarius burchardi, Spisula trigonella,* and *Tellina deltoidalis* for 21 sites, and Sites A1 and D20 were excluded. For 1986 data included *Arthritica semen, Bedeva paivae, Hydrococcus brazieri, Nassarius burchardi, Spisula trigonella,* and *Tellina deltoidalis* for all sites; *Acteocina* sp and *Bittium granarium* were excluded.

Results

Abundance trends

Analysis of the mean occurrences of molluscan fauna clearly indicates significant two-way interactions between species and times, as well as species and sites, but not between times and sites. Due to the significant two-way interactions, little can be said about the significant main effects. The model accounts for approximately 50% of the variation. The analysis of standardised residuals (Fig 2) showed departures from normality where the variation increases with the mean value, indicating that a logarithmic transformation of the data should be undertaken. Table 1 presents the results of the full analysis of transformed data, where all the two-way interactions are significant and the model accounts for 73% of the variation of the data. The log residual analysis (Fig 2) indicates a much closer alignment with the underlying normal distribution assumptions of the model. There are still a small number of residuals, which are either under, or over-estimated by the model and which may require closer investigation.

Using the log transformed data, further analyses highlights the trends in time and/or salinity and their effects on the mean occurrences of the species.

Table 1. Results of the analysis of log transformed mean occurrences

Source	Df	Deviance	Mean Deviance	F
species	6	1996.5	332.75	67.2***
times	10	240.5	24.05	4.9***
sites	11	648.8	58.98	11.9***
species x times	60	571.4	9.52	1.9***
species x sites	66	2422.3	36.70	7.4***
times x sites	85	544.9	6.41	ns
Residual	472	2337.4	4.95	
Total	**710**	**8761.8**		

* $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$; ns = not significant.

The results of the analysis of site groups are presented in Table 2. This analysis shows highly significant (< 0.1%) two-way interactions between species and site class with significant (5%) interactions for species by time and site class by time. The model accounts for approximately 55% of variation in the data.

Table 2. Results of the analysis of mean occurrences with grouped site classes

Source	Df	Deviance	Mean Deviance	F
species	6	1996.5	332.75	48.9***
times	10	240.5	24.05	3.5***
site class	3	271.1	90.37	13.3***
species x times	60	578.0	9.63	1.4*
species x site class	18	1373.9	76.33	11.2***
times x site class	28	321.8	11.49	1.7*
Residual	585	3980.0	6.80	
Total	**710**	**8761.8**		

* $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$.

The species by site class interaction indicates that the mean occurrences of species vary significantly with the site class. That is, some species are more prevalent at some of the site classes than others, showing in the along-estuary trend, some species are influenced by the salinity field gradient and might well be more salt-tolerant than others that are found further up the estuary.

The analysis of linear trend in site classes, using the indicator values (A -> 1, B-> 2, C -> 3, and D -> 4) is shown in Table 3. A significant positive (or negative) trend parameter would indicate that there is a gradient dependent on site class - that is, a salinity trend up (down) the estuary.

Table 3. Results of analysis of linear trends of grouped site classes

Source	Df	Deviance	Mean Deviance	F
species	6	1996.5	332.75	41.9***
times	10	240.5	24.05	3.0***
linear site trend	1	15.5	15.50	ns
species x times	60	579.7	9.66	ns
species x site trend	6	897.4	149.57	18.9***
times x site trend	10	136.7	13.67	ns
Residual	617	4895.4	7.93	
Total	**710**	**8761.8**		

* $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$ ns = not significant.

Table 3 illustrates a highly significant trend for species by linear site *i.e.* for individual species the trend across the estuary varies. Some species react more to the gradient in the salinity fields than others, with decreasing or increasing mean occurrences changing up (or down) the estuary. There are still significant differences between species and time.

The results of the analysis of linear time and site class trends, simplified by reducing the 10 degrees of freedom for time to a linear trend over time are shown in Table 4. Time has been "ordered" to indicate either a positive (or negative) linear trend, reflecting increases (or decreases) in overall species occurrences over the sampling time. Interactions, especially of species with time, would indicate that species occurrences are not consistent across time(s) *i.e.* some species may decrease over time while others remain stable or even increase.

Table 4. Results of analysis of linear trends of grouped site classes and time

Source	Df	Deviance	Mean Deviance	F
species	6	1996.5	332.75	41.1***
time trend	1	105.1	105.10	13.0***
site trend	1	15.9	15.90	ns
species x time trend	6	162.0	27.00	3.3**
species x site trend	6	893.3	148.88	18.4***
time x site trends	1	10.0	10.10	ns
Residual	689	5579.0	8.10	
Total	**710**	**8761.8**		

* $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$; ns = not significant.

This analysis indicates significant species by time and species by site class interactions. A further analysis which included a polynomial trend term for time indicated that the polynomial trend term is non-significant for time and can be eliminated from the model. The other significant interactions of species by linear time trend and species by linear site trend are still present.

The results of the final linear model includes the main effects of species, time trend and site class trend with interactions of species with time trend and species with site class trend (Table 5). No other effects have been included. In this model, all effects except the main effect of site classes are significant.

Table 5. Final analysis of occurrences

Source	Df	Deviance	Mean Deviance	F
NULL			8761.70	
species	6	1996.5	332.75	41.1***
time trend	1	105.1	105.10	13.0***
site trend	1	15.9	15.90	ns
species x time trend	6	162.0	27.00	3.3**
species x site trend	6	893.3	148.88	18.4***
Residual	690	5589.0	8.10	
Total	**710**	**8761.8**		

* $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$; ns = not significant.

The trends of abundance of the individual species over time using the final linear model are shown in Figs 4 & 5, with log-transformed predicted species abundance shown. for the four hydrochemical settings within the estuary in time. Fig 4 shows the patterns for the February data from each year, and Fig 5 shows the similar patterns for the May data. The patterns evident for each of the species are different in detail, showing variation in the rate of decrease or increase in overall populations numbers in time, and exhibiting small to large changes in abundance along the south to north estuarine gradient. *Acteocina* shows a very slight increase in relative abundance throughout the whole estuary in time, and there is a large and consistent contrast in abundance from south to north, with the species consistently more abundant in northern sites. *Arthritica* shows an evident decrease in relative abundance throughout the whole estuary in time, and there also is a small but consistent contrast in abundance from south to north, with the species consistently more abundant in northern sites. *Bedeva* shows a slight decrease in relative abundance throughout the whole estuary in time, and there is a relatively small but consistent contrast in abundance from south to north, with the species consistently more abundant in southern sites. *Hydrococcus* shows a very slight decrease in relative abundance throughout the whole estuary in time, and there is a large and consistent contrast in abundance from south to north, with the species consistently more abundant in northern sites. *Nassarius* shows a clear decrease in relative abundance throughout the whole estuary in time, and there is a very large and consistent contrast in abundance from south to north, with the species consistently more abundant in southern sites. *Spisula* shows a very marked decrease in relative abundance throughout the whole estuary in time, and there is a large and consistent contrast in abundance from south to north, with the species consistently more abundant in southern sites. *Tellina* shows a moderate decrease in relative abundance throughout the whole estuary in time, and there is a moderate and consistent contrast in abundance from south to north, with the species consistently more abundant in northern sites.

Clustering

The similarity/dissimilarity of the molluscan fauna sets derived from Flexible UPGMA Method for the years 1983-1986 shows the same patterns as described above. That is, predominately year to year variation in associations of mollusc species, with separations on the dendrogram for the different species occurring variably from year to year (Fig 5). However, there are three low-level associations: *Nassarius* and *Tellina* are associated in 1983, 1985 and 1986, though not 1984, separating on the similarity/dissimilarity axis at about 0.4 to 0.6; *Hydrococcus* and *Bittium* are weakly associated in 1984; and *Hydrococcus* and *Bedeva* are associated in 1986.

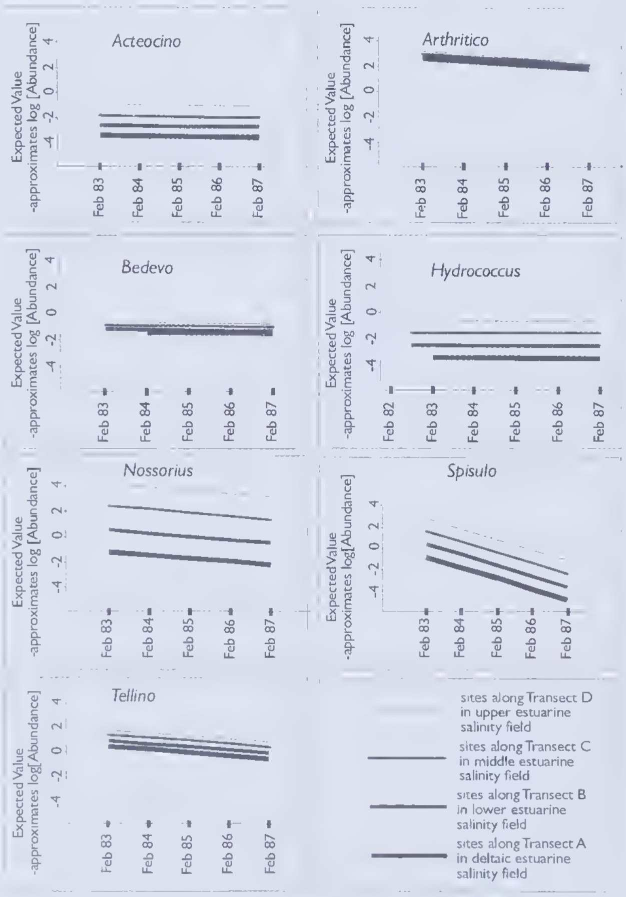

Figure 3: Graph of site class by time interaction for *Acteocina, Arthritica, Bedeva, Hydrococcus, Nassarius, Spisula* and *Tellina* for the sampling period February 1982 to February 1987. X-axis is time. Y-axis approximates log of abundance.

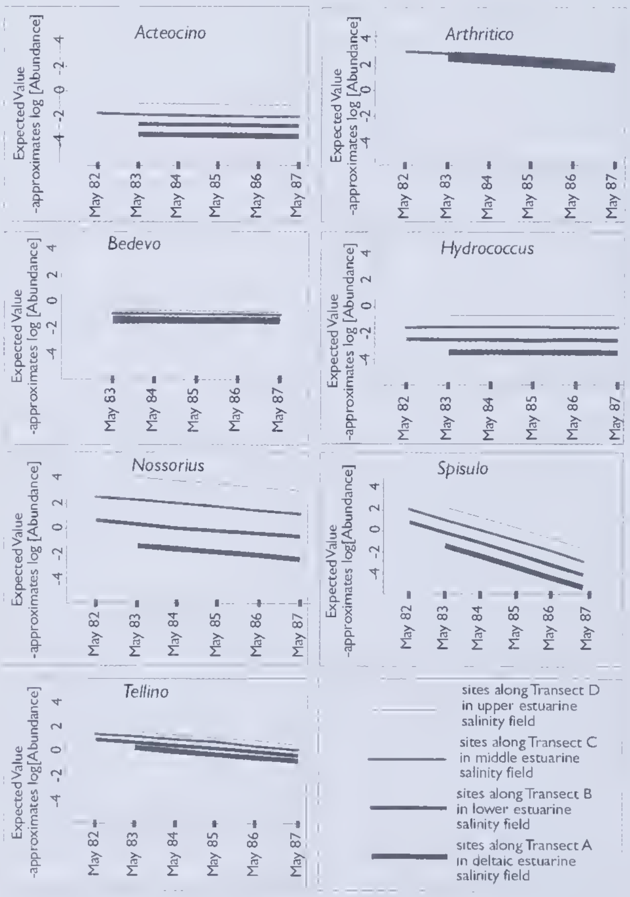

Figure 4: Graph of site class by time interaction for *Acteocina, Arthritica, Bedeva, Hydrococcus, Nassarius, Spisula* and *Tellina* for the sampling period May 1982 to May 1987. X-axis is time. Y-axis approximates log of abundance.

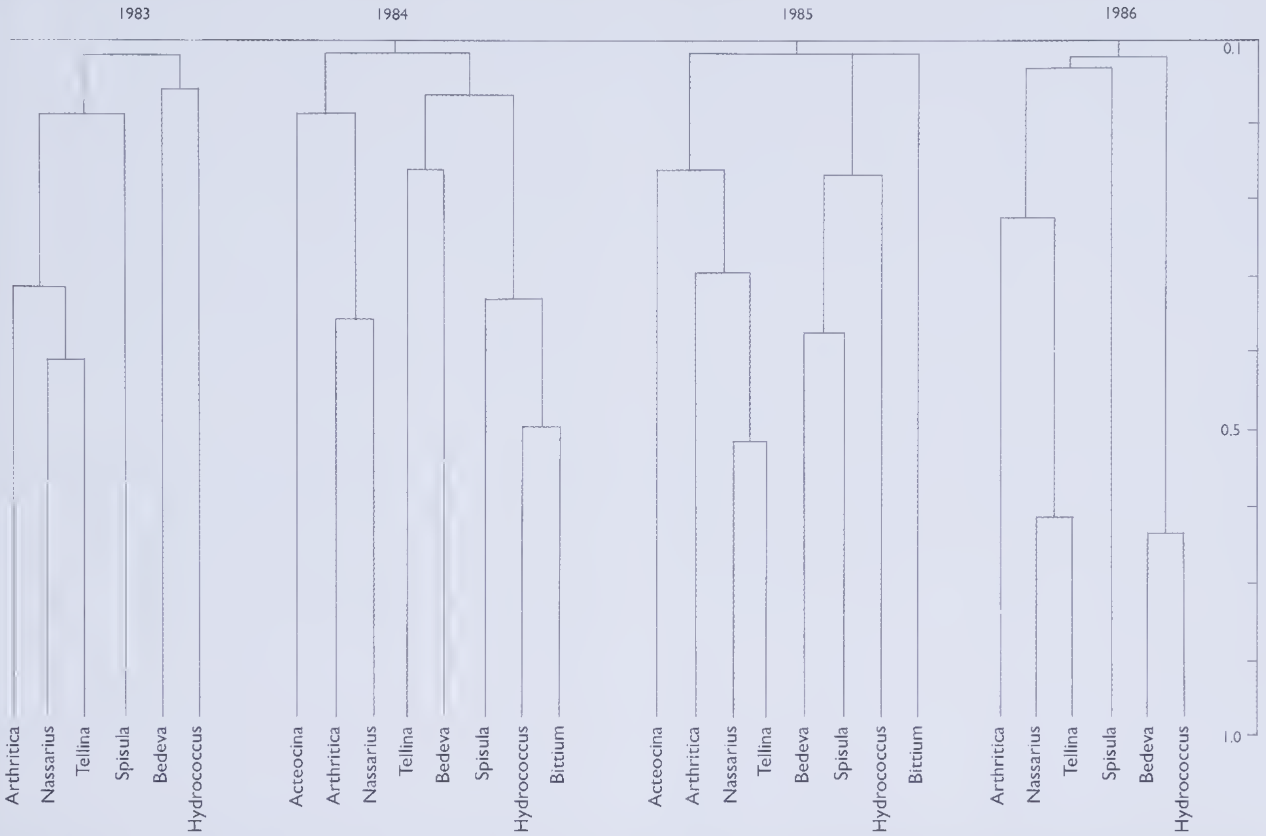

Figure 5. Dendrogram using Flexible UPGMA Strategy, for individual years between 1983-1986.

Discussion

Note should be made here that since only the February and May data were processed for each year, effectively using data from the summer months when the south to north gradient is at its most pronounced in terms of a transition from marine to hypersaline, the fluctuations in populations numbers brought about by freshwater and temperature effects are eliminated. The trends in the graphs thus illustrate an underlying pattern in the population numbers. Also, patterns derived from data for both February and May each year are similar.

Our analyses of mollusc abundance trends, both spatially and temporally, had an objective of summarising the responses of the various species as succinctly as possible to interpret the species responses. This has been achieved by looking for trends within time and/or sites (response to the south to north salinity gradient in the estuary) for each species. The final linear model does not account for as much variation in the data as more complex models but provides a simple interpretation of the responses.

The hydrochemical setting with its south to north gradient provides a framework to interpreting species distribution. While allocation of sampling sites to estuarine salinity fields reflects a gradient of increasing salinity, with A being marine to freshwater, B being mainly marine, and C and D reflecting a wider salinity fluctuation with salinities becoming progressively more saline and hypersaline for parts of the hydrologic cycle, the gradient also may reflect other changes in hydrochemistry in the estuarine waters, in that nutrient content and turbidity may be linked to fluvial influx and bathymetry of the estuary. However, for purposes of this paper, the hydrochemical gradient is considered to be the main factor, and in the discussions that follow the gradient from south to north in the estuary is referred to as the "salinity gradient".

The analysis of species by times by sites clearly indicates there to be significant time and/or site trends within the data (the latter reflecting the hydrochemical gradient, or salinity). These trends are significantly species-specific, which is to be expected since some species are more marine in character and opportunise the estuary during appropriate times of the hydrochemical cycle, than others. Some species respond to both time and salinity (site) levels while other species may show only a response to either time or salinity gradient, but not both.

Almost all of the species show an effect of site or salinity (*i.e.* location in the prevailing estuarine salinity field), but this varies markedly between the species. *Arthritica* and *Bedeva* show a minimal difference or effect of site (salinity), and only small decreases in mean count over time. However, *Spisula* and *Tellina* show much larger effects of changes over the gradient and over time, with *Spisula* being strongly influenced by the prevailing salinity gradient. This effect of location within the estuary, related to the salinity gradient may be due to the prevailing gradient in salinity, or nutrient content, or some other expression of the hydrochemical field, *e.g.* phytoplankton), or combinations of these (Semeniuk &

Wurm 2000). Progressing along the estuary from A to B, C and then D, there is a marked decrease in the mean count for these two species, reflecting their preference for more marine conditions, and potential intolerance of hypersaline conditions. There is also a marked decrease in counts, for all sites, over the time of the study, a factor that related to the overall long-term population dynamics of the species in response to longer-term patterns of estuarine environments (*e.g.* increase or decrease in nutrient enrichment, or volumes of freshwater influx on a 20-year cycle, amongst others).

The relationship between location (salinity) and abundance described above is also evident for *Nassarius*. However, for this species the decline with time is much less noticeable than for *Spisula*. *Tellina*, on the other hand, shows the reverse trend for site. The mean counts increase as the salinity level increases up the estuary. Again, there is a decrease in the mean count over the term of the study, but this decline in count over time is much less noticeable that the decline associated with *Spisula*. The final two species, *Acteocina* and *Hydrococcus* have site responses similar to *Arthritica*, but only very small response to time.

In summary, the seven mollusc species can be assigned to two groups on the basis of their responses to the south to north gradient along the estuary:

1. The first group consists of *Arthritica*, *Acteocina*, *Hydrococcus* and *Tellina*; which has had a positive response to the south-to-north gradient. The level of this response varies markedly between the four species, with *Arthritica* exhibiting almost no differences between sites, *Tellina* exhibiting a larger between-site effect, whereas *Acteocina* and *Hydrococcus* show marked effects of site differences. *Arthritica* and *Tellina* indicate a decrease over time whereas the other two species show little if any effect of time.
2. The second group consists of *Bedeva*, *Nassarius* and *Spisula*; which has a negative response to the south-. to-north gradient. The mean counts decrease markedly, especially for *Nassarius* and *Spisula* as salinity increases. *Nassarius* and *Spisula* have marked time effects with counts decreasing over time. There is only a slight trend in time for *Bedeva*.

These contrasts in temporal and spatial patterns will result in varying assemblages at a given time. That is, given there are positive *vs* negative trends of abundance for the different species along the south to north estuarine gradient, as well as decreases *vs* increases in abundance in time, and different rates of change (rapid decrease *vs* negligible decrease), it follows that assemblages determined by the present/ absence, and relative abundance of the principal species of mollusc will be highly variable from year to year.

The dendrogram shows year to year changes in abundance of mollusc species such that different aggregation of species would result from data used at one particular time to that used from another. For example, the assemblage groupings arising from data for February 1983 are different to those arising from data for February 1984. This would indicate that researchers must exercise caution in using results from one year, or even several years, to categorise biotic assemblages mathematically within environments such as estuaries that exhibit a marked level of hydrochemical and biotic dynamism. Our conclusion is that the attempt to categorise the mollusc fauna mathematically in "assemblage" failed largely because there are no clear associations. The most marked and consistent association appear to be for *Nassarius* and *Tellina*, but this association was not consistent for all years.

One of the interesting features to emerge from these mathematical analyses is that the results of the spatial and temporal analyses of abundance could be used from first principles to derive the various assemblages with their variable faunal compositions from year to year. This would indicate marked intra-assemblage variability from year to year, patterns that are evident and corroborated by the dendrogram. Overall, it would seem that mathematical and cluster analyses of biotically dynamic systems should be confined to autoecological analyses until the larger holistic patterns are well understood.

The crucial factors underpinning the inter-annual variability in faunal "communities" is the dynamic nature of the estuarine environment. Aspects of variation in habitats temporally influencing biotic assemblages and changing species associations in time are explored and discussed by Austin (1985). For the Leschenault Inlet estuary, there are changes in estuarine hydrochemistry from year to year (reflecting, for instance, inter-annual and inter-decadal rainfall variability in the environment and in the catchment, and variable loading of anthropogenic nutrient). There is inter-annual variability in hydrodynamics, driven by wind and storms (affecting sediment transport and sedimentation). There is variability in the population dynamics of primary producers (with influx and intra-estuarine dispersion of floating marine algae, the growth and contraction of seagrass beds, the increase and decrease in plankton) and its concomitant effects on epibenthic and infaunal biota), and variability in the recruitment, migration, mortality rates, of benthos.

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Appendix 1. Mean abundance of mollusc species per metre square for the various sites and times used in this study

	A2	A3	A4	B9	B11	B12	C15	C17	C19	D20	D21	D22
Acteocina												
Feb-82	*	*	*	0	*	0	*	*	*	*	*	*
May-82	0	0	0	0	0	0	0	0	170	0	0	0
Feb-83	0	0	0	0	0	0	9.6	0	0	9.6	3.2	13
May-83	0	0	0	0	0	*	0	0	0	3.2	3.2	*
Feb-84	0	0	0	0	0	0	58	0	38	19	13	90
May-84	0	0	0	0	0	*	3.2	0	45	26	9.6	9.6
Feb-85	0	0	0	0	0	0	16	0	32	0	32	22
May-85	0	0	0	0	0	*	0	0	0	0	0	6.4
Feb-86	0	0	0	0	0	0	0	0	0	0	0	0
May-86	0	0	0	0	0	0	0	0	0	0	0	0
Feb-87	0	0	0	0	0	*	0	0	0	106	67	112
Arthritica semen												
Feb-82	*	*	*	*	*	*	*	*	*	*	*	*
May-82	0	0	127	1529	510	0	662	1885	25	51	1885	255
Feb-83	3159	0	76	688	0	0	917	4637	*	3159	16052	127
May-83	892	0	178	408	51	*	1248	1885	*	382	*	*
Feb-84	178	0	382	382	102	0	2675	357	408	1987	7924	1223
May-84	0	0	0	535	0	*	0	0	*	229	994	1554
Feb-85	51	0	102	178	306	0	0	0	0	0	153	0
May-85	1147	408	280	0	153	*	153	153	*	1172	815	917
Feb-86	51	204	51	76	0	0	229	255	0	0	127	0
May-86	204	153	25	96	25	0	76	280	0	0	127	0
Jan-87	5657	1987	1350	764	1198	*	917	2548	*	2370	10217	484
Feb-87	76	357	0	1427	0	*	0	4383	*	11415	13606	0
Bedeva paivae												
Feb-82	*	*	*	1.6	*	0	*	*	*	*	*	*
May-82	0	0	0	0	0	0	0	6.4	3.2	0	0	0
Feb-83	0	9.6	0	6.4	0	0	3.2	3.2	0	0	0	0
May-83	9.6	0	0	0	0	*	0	13	0	0	0	*
Feb-84	0	35	0	0	0	0	3.2	0	0	0	0	0
May-84	0	0	0	0	0	*	0	3.2	3.2	0	0	0
Feb-85	0	3.2	0	32	0	3.2	0	0	6.4	0	0	0
May-85	6.4	0	0	3.2	0	*	0	0	0	0	0	0
Feb-86	0	0	0	3.2	0	0	0	0	0	0	0	0
May-86	0	0	0	9.6	0	0	0	0	0	0	0	0
Jan-87	0	3.2	0	6.4	3.2	0	0	3.2	0	0	0	0
Feb-87	3.2	0	0	16	0	*	6.4	0	0	0	0	0
Hydrococcus brazieri												
Feb-82	*	*	*	0	*	0	*	*	*	*	*	*
May-82	0	0	0	0	0	0	0	0	3974	0	0	0
Feb-83	0	0	0	0	0	0	6.4	0	15008	9.6	3.2	0
May-83	0	0	0	0	0	*	0	0	0	0	3.2	*
Feb-84	0	0	3.2	3.2	0	0	0	0	0	3.2	9.6	6.4
May-84	0	0	0	0	0	*	99	0	32	0	3.2	0
Feb-85	0	0	0	0	0	0	0	0	0	0	0	0
May-85	0	0	0	0	0	*	32	0	9.6	0	38	6.4
Feb-86	0	0	0	0	0	0	3.2	0	0	0	0	0
May-86	0	0	0	0	0	0	9.6	0	0	0	0	0
Feb-87	0	0	0	0	0	*	0	0	109	35	3.2	3.2
Nassarius burchardi												
Feb-82	*	*	*	93	*	6.4	*	*	*	*	*	*
May-82	154	32	486	77	29	42	32	6.4	0	0	0	0
Feb-83	285	250	1446	387	211	198	32	154	0	0	0	0
May-83	474	256	1338	374	93	93	19	51	0	0	0	*
Feb-84	3.2	74	938	381	32	38	45	115	0	0	0	0
May-84	9.6	16	301	35	64	*	0	26	0	0	0	0

Appendix 1 (continued). Mean abundance of mollusc species per metre square for the various sites and times used in this study

	A2	A3	A4	B9	B11	B12	C15	C17	C19	D20	D21	D22
Nassarius burchardi												
Feb-85	32	22	3.2	387	61	22	3.2	80	0	0	0	0
May-85	22	19	13	42	42	*	0	70	9.6	0	0	0
Feb-86	9.6	0	42	48	6.4	*	0	9.6	3.2	0	0	3.2
May-86	74	0	6.4	202	9.6	*	9.6	9.6	9.6	0	0	6.4
Feb-87	6.4	26	42	154	38	*	38	74	3.2	0	0	0
Spisula trigonella												
Feb-82	*	*	*	1.6	*	3.2	*	*	*	*	*	*
May-82	570	512	0	0	6682	11958	0	13504	45	0	0	0
Feb-83	1222	2326	0	0	5570	4384	0	2880	42	0	0	0
May-83	1107	2774	3.2	0	3456	3296	0	1760	35	0	0	*
Feb-84	0	1078	0	0	38	3.2	0	0	0	0	0	0
May-84	9.6	0	0	0	0	*	0	0	0	0	0	0
Feb-85	0	3.2	3.2	0	3.2	3.2	0	0	0	0	0	0
May-85	9.6	0	0	0	0	*	0	0	0	0	0	3.2
Feb-86	0	0	0	0	0	0	0	0	0	0	0	0
May-86	6.4	0	0	0	0	0	0	0	0	0	0	0
Feb-87	3.2	0	0	0	0	*	0	0	0	0	0	0
Tellina deltoidalis												
Feb-82	*	*	*	59	*	94	*	*	*	*	*	*
May-82	0	29	83	80	48	154	61	58	3.2	0	35	0
Feb-83	0	22	166	198	77	102	70	86	0	6.4	13	6.4
May-83	3.2	6.4	154	123	48	*	38	80	3.2	3.2	6.4	*
Feb-84	0	6.4	266	96	80	83	83	90	0	26	3.2	0
May-84	0	0	102	6.4	77	*	32	96	0	64	6.4	9.6
Feb-85	0	67	106	70	138	67	13	118	6.4	0	18	22
May-85	0	0	32	6.4	0	*	0	6.4	0	26	0	0
Feb-86	0	0	32	38	16	67	0	0	3.2	9.6	42	67
May-86	0	0	29	19	3.2	61	13	0	0	26	45	61
Feb-87	0	3.2	83	154	38	*	38	74	3.2	16	0	3.2
Mar-87	0	6.4	80	125	45	58	106	29	6.4	13	3.2	0